

## The Relictual Fern Genus *Loxsomopsis*

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**ABSTRACT.**—We conducted a systematic revision of the genus *Loxsomopsis* H. Christ (Loxomataceae) based on 99 herbarium sheets representing about 52 separate gatherings. Many morphological characters varied considerably, but as much of this variation was found within individual collections it was of little taxonomic relevance. Characters that varied between specimens but remained roughly constant within individual gatherings included the pubescence of lamina, petiole, and sorus, hair size and coloration, presence or absence of glaucous layers on the lamina surface, and spore surface structure. However, we found no correlation in the occurrence of two or more of these characters and were unable to morphologically define discrete species within the genus. Thus, we consider *Loxsomopsis* to include one variable species, *L. pearcei* (Baker) Maxon. The morphological variation is probably the result of the distribution of the species in small, isolated populations in ephemeral early successional habitats, leading to continuous population extinction and establishment of new population based on few propagules. Notes on ecology and distribution, full taxonomy, and specimen citations are provided.

*Loxsomopsis* Christ is the Neotropical representative of the relictual and taxonomically isolated fern family Loxomataceae, whose other genus, *Loxoma*, is restricted to the North Island of New Zealand. *Loxsomopsis* is distinguished from *Loxoma* principally by its sporangia in which about two-thirds of the annulus cells are thickened (vs. only the apical cells thickened) and which open transversely (vs. longitudinally). After considerable debate as to the taxonomic relationships of the family (Tryon and Tryon, 1982; Kramer, 1990), it is now believed to be related to the tree fern alliance, along with Cyatheaceae, Dicksoniaceae, Lophosoriaceae, and Metaxyaceae on the basis of anatomical, morphological, and molecular characters (Markham and Given, 1979; Stevenson and Loconte, 1996; A.R. Smith, pers. comm.).

The genus *Loxsomopsis* was described by Christ (1904) based on *L. costaricensis* from Costa Rica, but the first species was actually described in 1891 by Baker as *Dicksonia pearcei* from Ecuador and was transferred to *Loxsomopsis* by Maxon in 1933. Two further species have been described, *L. lehmannii* from Ecuador by Hieronymus in 1904, and *L. notabilis* from Bolivia by Slosson in 1912. Because of the distinctness of the genus, there has been little debate about the generic delimitation and the placement of individual species. The delimitation of the species, however, is less clearcut and it has been suggested that only one species should be recognized (Tryon and Tryon, 1982; Tryon and Stolze, 1989). Overall, *Loxsomopsis* appears to be rare and/or localized in the field and is poorly represented in herbaria. A modern treatment for the genus is lacking. The present study is an outcome of a course on pteridophyte taxonomy and systematics and is based on a morphological anal-

ysis of 99 herbarium sheets of *Loxsomopsis* representing about 52 separate gatherings from 15 herbaria.

#### MORPHOLOGICAL CHARACTERS

*Stems.*—Stems are terrestrial, long-creeping, dichotomously branched, dark brown, 1.5–5 mm in diameter, and with internodes 1–7 cm long. Scattered, dark, fibrous roots are produced from all sides. A physical relationship of the roots to the leaf bases was not noticed. Stems are densely pubescent with stiff bristles (defined as in Lellinger, 1985, by having pluriseriate bases and an uniseriate apex) that are dark brown, 0.8–2.4 mm long, basally pluriseriate with about 8–16 cells, and with an uniseriate apex consisting of 3–25 cells (Fig. 1A). The entire variation of bristle length and cell number can be found on individual stems. Presumably depending on the growth location, bristles can be erect or appressed, with both conditions as well as intermediates present on the same stem. The stems are solenostelic (Ogura, 1972). Root cortex anatomy corresponds to the *Osmunda*-type (Schneider, 1996), with a hypodermis of sclereids and inner cortical layers formed by relatively thin-walled cells.

*Petioles, rhachises and costae.*—Petioles are adaxially convex to flattened-sulcate and 0.6–4 mm in diameter. Coloration varies from dark blackish or reddish brown to pale olivaceous brown, with the proximal portion generally being darker. The proximal 1–2 cm of the petioles are generally densely covered in bristles resembling those of the stem. Scattered bristles are also found further along the petioles, especially in the groove. Frequently, petiole bristles have been abraded, leaving raised multicellular scars. Petiole length comprises about 45% to 65% of the entire leaf length. A single, gutter-shaped vascular bundle arrangement is present in the petioles (Kramer, 1990).

Rhachises are similar to the petiole, but tend to be somewhat more strongly sulcate, the groove more pronounced in dry than in fresh material. Rhachis coloration is generally paler than that of the petiole and is markedly darker on the adaxial than on the abaxial side. The costae, when dry, are rounded to slightly sulcate with a brown base and pale yellowish medial and distal portions. Scattered hairs (defined as in Lellinger, 1985, as being uniseriate throughout), resembling those of the lamina, occur occasionally on the costae.

*Laminae.*—Leaves are monomorphic, catadromous, subcoriaceous, circinate in the bud, and with lamina length varying from 0.2 to 1.5 m. Leaf lengths of 5 m reported by Tryon and Tryon (1982) and Tryon and Stolze (1989) were not evident in herbarium material available to us nor observed in the field (M. Kessler, pers. obs., M. Lehnert, pers. obs.). Leaf dissection varies from 1-pinnate-pinnatifid on small leaves to bipinnate-pinnatifid on the largest leaves (Fig. 2). The pinnae are (sub)sessile, well-spaced, subopposite, asymmetric, with the proximal pinnae generally being the longest, reaching about 50% of the lamina length resulting in a narrowly to broadly deltate lamina outline. Secondary pinnae and segments are obliquely ascending, decurrent, with crenate to entire margins, and with the ultimate segments deltate-lanceolate. On

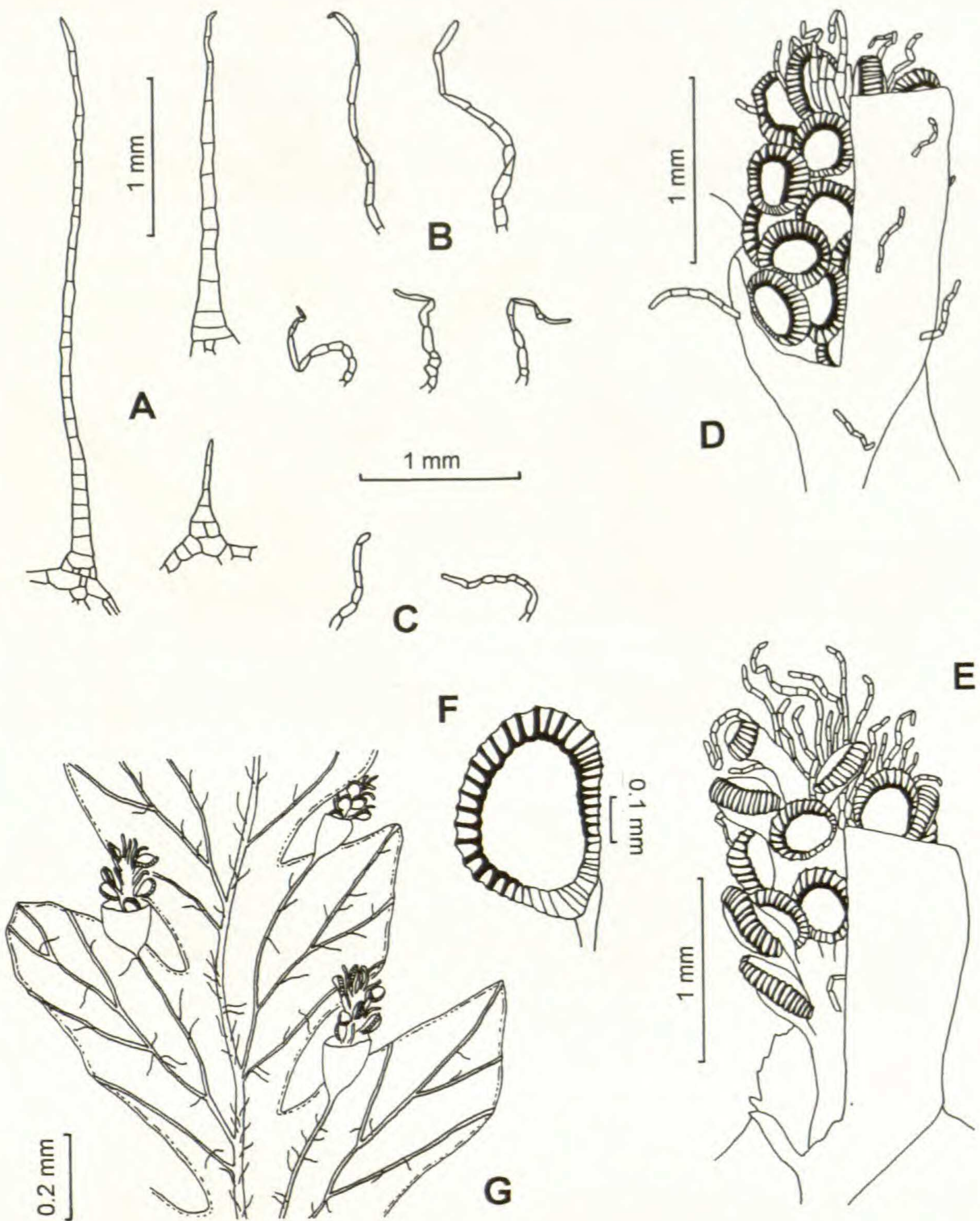


FIG. 1. Morphological details of *Loxsomopsis pearcei*. A) Stem bristles, showing variability in size and cell number, *Moran 3057*; B) Variability of lamina surface hairs, *Moran 3057*; C) Hairs from indusium, *Moran 3057*; D) Young sorus with short receptacle and sporangial stalks; left side of hairy indusium removed, *Øllgaard 74387*; E) Ripe sorus with lengthened receptacle and sporangial stalks; left side of glabrous indusium removed, *Lent 738*; F) Sporangium, showing the subvertical annulus with about  $\frac{3}{4}$  of the cells indurated, *Øllgaard 74387*; G) Detail of pinna, showing free, forked-subpinnate venation, sorus location on vein ending at lamina margin, and pubescence on adaxial side, *Goldgewicht 86369*.

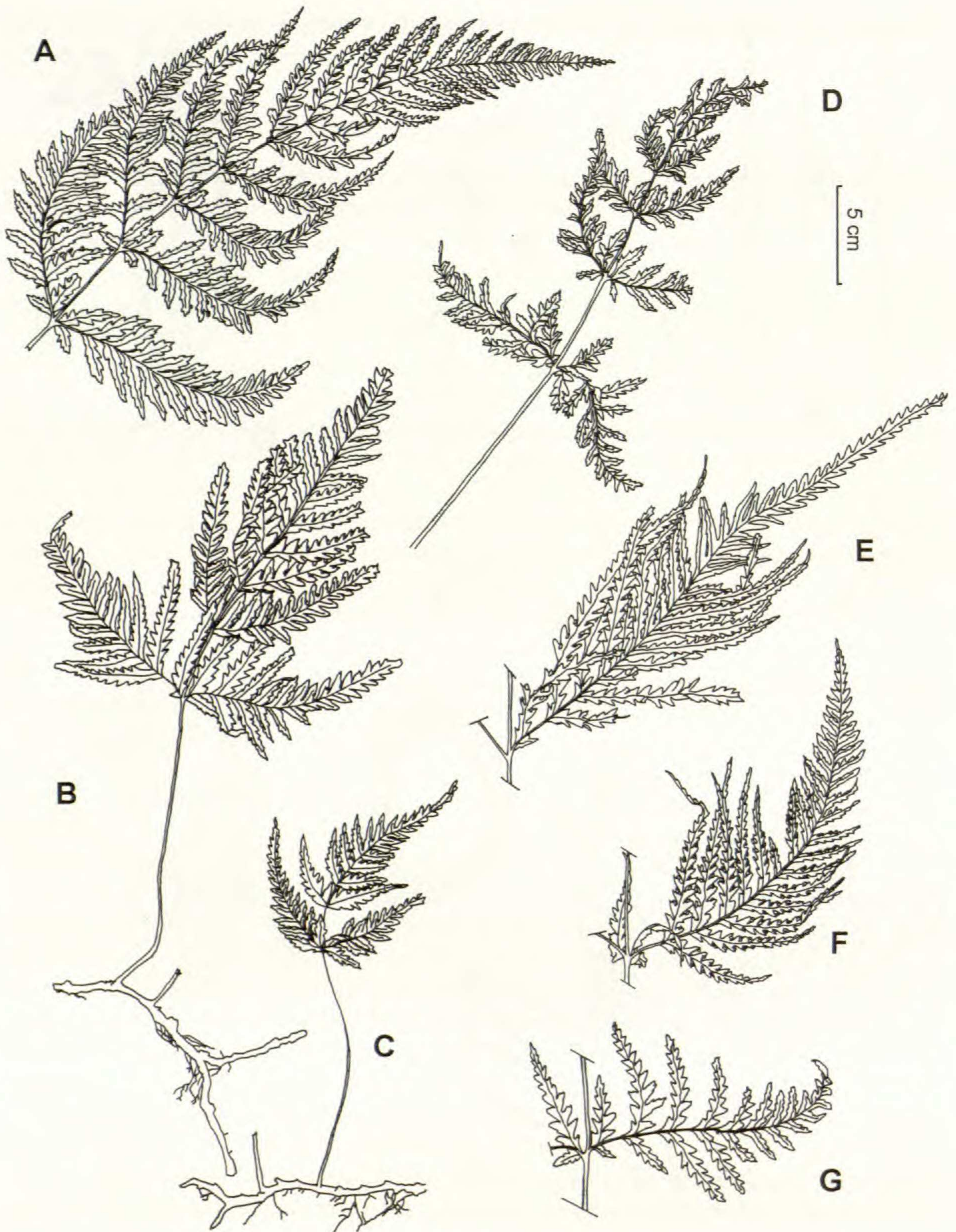


FIG. 2. Variability of lamina size, dissection, and shape. A) Distal portion of a large leaf, shown without the three proximal pinna pairs, *Grayum* 7212; B) Fully-developed, fertile, mid-sized leaf, *Prieto* 259; C) Fully developed, sterile, very small leaf, *Øllgaard* 90634B; D) Mid-sized leaf with notably differing segment shape, *Lehmann* 5715; E–G) Proximal pinnae showing differences in degree of dissection, segment orientation, and shape, *Lehmann* 5059, *Goldgewicht* 86369, *Goldgewicht* 863.

fertile leaves, acroscopic first- and second-order segments are larger than their basiscopic counterparts, whereas on sterile leaves they can occasionally be of similar size. Degree of lamina dissection, shape of pinnae and pinnules, and orientation of the pinnae vary considerably between leaves and individuals (Fig. 2). Smaller leaves tend to have longer, narrower, ascending pinnae, whereas larger leaves tend to have broader, more spreading pinnae. During lamina development, segments tend to be more rounded than on mature leaves. Veins are free, forked-subpinnate and catadromously branched (Fig. 1).

Laminae of *Loxsomopsis* can be glabrous to densely pubescent abaxially with uniseriate, up to 2 mm long, light to brown, tortuous, septate hairs (Fig. 1). The frequency and coloration of this vestiture varies geographically, with Costa Rican specimens characterized by long, pale hairs whereas specimens from some Ecuadorean locations have dark brown hairs. Bolivian specimens tend to have a glaucous abaxial lamina surface which varies among and within collections (Tryon and Stolze, 1989). Field observations have shown that older laminae are more glaucous than younger ones (M. Lehnert, pers. obs.). Adaxially the laminae are always glabrous.

*Sori*.—Sori of *Loxsomopsis* are located marginally on veins and are directed downward from the lamina surface. Generally, a single sorus is located on the acroscopic side of each terminal pinnule or ultimate segment, although occasionally a second sorus is found basiscopicly. Sori are narrowly cyathiform to urceolate and have a laterally free and protruding indusium with an entire rim. Superficially, they resemble sori of the Hymenophyllaceae. Indusia are glabrous to sparsely pubescent with hairs (Fig. 1D) resembling those of the laminae (Fig. 1C).

Sporangia and paraphyses are borne on a columnar receptacle whose basal portion elongates during sorus maturation, eventually measuring as much as 50% of the entire indusium length (Fig. 1D, E). As a result, young sori have fairly narrow indusia which conceal most of the sporangia, whereas in mature sori the majority of sporangia protrude beyond the more open indusium. Ripe sori are about 1 mm wide and 1.75–2.75 mm long. Paraphyses are uniseriate, unbranched, and without thickened cells, 0.5–0.8 mm long, and consist of 5–10 cells which are about 2–3 times longer than wide.

*Sporangia*.—The number of sporangia per sorus varies from (10)15 to 30(50), with much of this variation found on single leaves. Sporangia are borne on short, ca. 6-rowed stalks that lengthen somewhat during sorus maturation. Sporangia are more or less pyriform (Fig. 1F), about 350  $\mu\text{m}$  wide and 450  $\mu\text{m}$  long, with very little variation in size among and between collections. The annulus is complete, almost vertical, bypasses the stalk, and consists of 30 to 55 cells. Annular cells are indurated, except for a group of laterobasal cells which are smaller and have thinner cell walls. These thin-walled cells make up about 1/4 of the annulus (Fig. 1F).

*Spores*.—Spores of *Loxsomopsis* are trilete, tetrahedral-globose with prominent angles, with the laesure 1/2 to nearly equal the spore radius, and lack chlorophyll. Spores are 41–62  $\mu\text{m}$  in diameter, with much of this variation found in single sori, e.g., 41–60  $\mu\text{m}$  ( $n = 20$ , mean = 54  $\mu\text{m}$ ) measured in

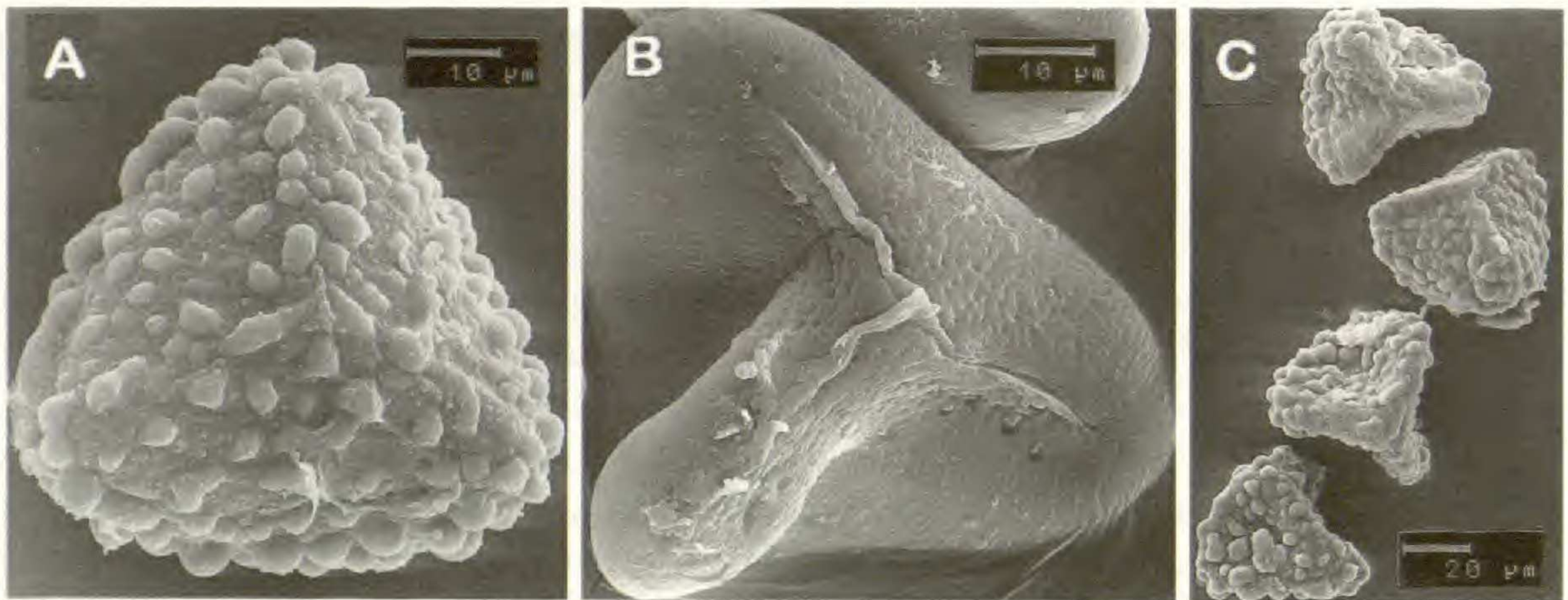


FIG. 3. Spores of *Loxsomopsis pearcei*. A) Verrucate spore with irregular granular deposit, *Goldgewicht 86369*; B) Slightly pitted spore, *Moran 3051*; C) Variability of surface structuring in verrucate spores, *Øllgaard 9479*.

*Goldgewicht 86369*. In three cases (*Bües 2119*, *Harling 24597*, *Lent 738*) the number of spores per sporangium was determined to be 128. Spore surface is slightly pitted (Fig. 3B) to strongly verrucose (nomenclature after Lellinger and Taylor, 1997) with distinct humps or longish, coalescent ridges (Fig. 3A; see also Tryon and Lugardon, 1991:213). These structures are formed by a two-layered perispore (Tryon and Lugardon, 1991). Spores derived from a single specimen are generally similar, but there is some variation in the degree of coalescence of the tubercles (Fig. 3C). The spores are often, but not always, covered with an irregular granular deposit (Fig. 3A).

*Gametophytes*.—Gametophytes of *Loxsomopsis* were described by Stokey and Atkinson (1956). They are epigeal, chlorophyllous, obcordate to somewhat elongate, centrally thickened, with thin margins, and bear long, multicellular hairs. Archegonia are borne on the lower surface of the thickened portion, especially apically, with the several- to many-celled antheridia located on the lower surface, and less often on the upper surface.

*Chromosome number*.—*Loxsomopsis* has been reported as  $n = 46$  from Cerro Vueltas, Costa Rica, by Wagner (1980).

#### TAXONOMIC CONSIDERATIONS

Numerous morphological characters exhibited considerable variation. Many of these characters varied as much within as between collections and were thus of little taxonomic relevance. Such characters include overall leaf size, stem and petiole diameters, relative petiole length, degree and shape of lamina dissection, size of the stem and petiole bristles, the number of annulus cells, the number of sporangia per sorus, and spore size.

Characters that varied between specimens but remained roughly constant within individual gatherings included the pubescence of lamina, petiole, and sorus, hair size and coloration, presence or absence of glaucous layers on the lamina surface, and spore surface structure. However, we were unable to find

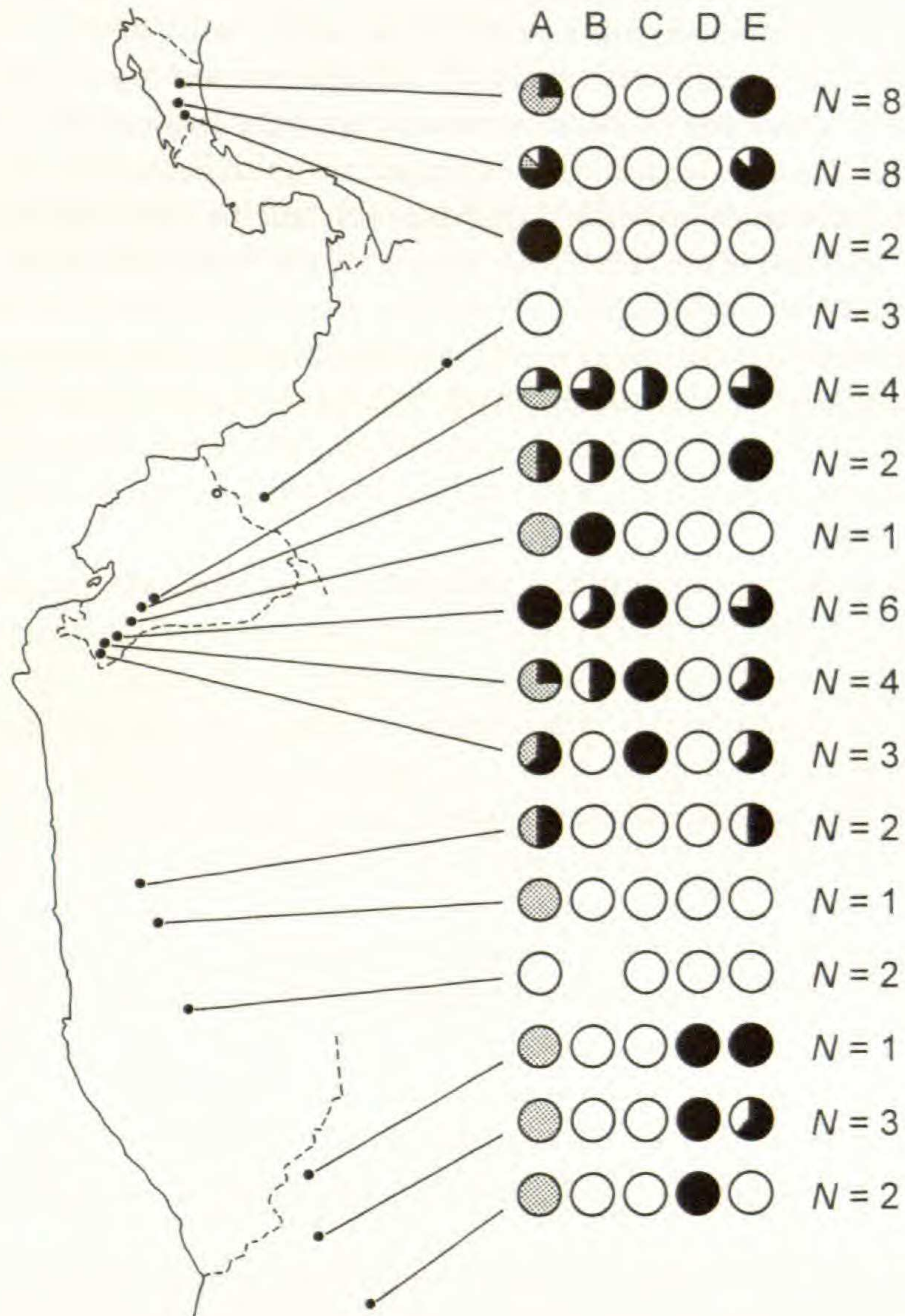


FIG. 4. Geographical distribution of several variable morphological characters among 52 gatherings of *Loxsomopsis pearcei* from 21 localities, indicating the number of gatherings per site (*N*). Characters and character states: A) Lamina pubescence: white: glabrous, gray: slight, black: dense (petiole pubescence followed the same pattern and is thus not shown as an independent character). B) Lamina hair coloration: white: pale, black: brown. C) Indusium pubescence: white: glabrous, black: hairy. D) Glaucous lamina surface: white: absent, black: present. E) Spore surface: white: smooth to slightly pitted, black: verrucose. Due to sterile or incomplete material, not every gathering has been considered for each character. The open circle shows the locality of a specimen not studied by us (*Palacios and Clark 12463 (MO)*).

a correlation among these independent characters. There were some noticeable geographic trends, but exceptions were also found (Fig. 4). For example, Costa Rican specimens are characterized by rather long, pale and frequently abundant lamina hairs, but one specimen (*Evans 2660A*) was completely glabrous. Furthermore, the vestiture of some Ecuadorian and Peruvian collections re-

sembled that of the Costa Rican specimens. Dark brown hairs were restricted to Ecuadorian populations, but occurred in only about 60% of the specimens examined. Bolivian specimens were all characterized by a glaucous abaxial lamina surface. Pubescent indusia were found only in Ecuador, but not among all specimens from the region. The conspicuous differences in spore surface structure were specimen-specific and not related to the developmental stage of the spores, as has been reported, e.g., among Polypodiaceae (van Uffelen, 1997). None of these geographical trends were correlated with variation in other independent characters. Overall, the apparent independence of character variation precludes the delimitation of multiple taxa within *Loxsomopsis*. A comparable situation of a variable species which cannot convincingly be divided into discrete species is presented by *Plagiogyria semicordata* (Zhang and Nootboom, 1998).

While cytological or molecular analyses are lacking, we found no evidence to suggest that different ploidy levels are represented within *Loxsomopsis*. Spore size varied as much within as between individuals and we found no individuals with consistently malformed or abortive spores that would indicate hybridization between plants of different ploidy levels.

We interpret the considerable morphological variation among different populations of *Loxsomopsis* to be a result of the localized and ephemeral nature of the growth sites of the species and its overall rarity. Since *Loxsomopsis* occurs mostly on disturbed sites such as landslides and roadsides, new populations are presumably regularly formed and then quickly lost as conditions are altered during vegetation succession. The result is a dynamic metapopulation structure in which new populations are frequently formed by one or few spores (Eriksson, 1996). Such a population structure would favor genetic drift and would explain the independent variation of morphological characters.

In summary, we have been unable to detect any character combinations that would permit the delimitation of different taxa within *Loxsomopsis*. While we cannot rule out the possibility that *Loxsomopsis* includes cryptospecies, we have found no evidence to support this assumption and consider the genus to include a single variable species, *Loxsomopsis pearcei*.

#### GEOGRAPHIC DISTRIBUTION

*Loxsomopsis* is known from Costa Rica, Colombia, Ecuador, Peru, and Bolivia (Fig. 4). In Costa Rica, *Loxsomopsis* is confined to three separate populations, corresponding to the volcanoes Poas and Barva, and to the Cordillera de Talamanca. In Colombia, specimens have been obtained from the eastern Andean chain near the Venezuelan border and from both sides of the Andes close to the Ecuadorean boundary. While not yet known from Venezuela, the species may well occur there. In Ecuador, there is one specimen of *Loxsomopsis* from the northwestern Andean slope, but most collection come from the central and southern portion of the eastern Andean slope, where it has been collected along all major roads traversing the region, and presumably occurs



as one fairly large, nearly continuous population. The species appears to be absent from the botanically rather well-known northern portion of the eastern versant. In Peru, *Loxsomopsis* has been collected at three scattered localities in the central portion the country. Its absence from northern Peru, including several well-collected localities in the departments Amazonas and San Martin may well represent a real distributional gap. In contrast, the lack of collections from southern Peru may be a result of the low collecting activity in the region. In Bolivia, there are three known localities for *Loxsomopsis*, two of which, the La Paz-Coroico and the Cochabamba-Villa Tunari roads, correspond to the most intensively studied areas in the country. We suspect that *Loxsomopsis* occurs in intermediate areas as well.

#### ECOLOGY

*Loxsomopsis* has been collected between about 1950 m and 2700 m in Costa Rica, and between 1800 m and 3600 m in the Andes. The majority of specimens have been gathered from roadside and forest edge habitats, but numerous specimens from Volcan Poás in Costa Rica have been found along the margin of the volcanic crater lake. Tryon and Tryon (1982) cite open habitats in ravines, on brushy slopes and open woodland as growth sites for *Loxsomopsis*. In the Andes, *Loxsomopsis* occurs on slopes disturbed by landslides and along roadsides, growing syntopically with aggressive colonizing ferns of the genera *Sticherus* (Gleicheniaceae) and *Hypolepis* (Dennstaedtiaceae) with which it forms dense tangles (León and Young, 1996, M. Kessler and M. Lehnert, pers. obs.). Leaves of *Loxsomopsis* are sometimes long with a pendent apical portion and lean on adjacent shrubby plants (Tryon and Tryon, 1982). *Loxsomopsis* has been collected on a wide variety of geological substrates, ranging from volcanic soils in Costa Rica to sandy soils and lutites in the Andes.

Generally, *Loxsomopsis* appears to be rather rare. In Bolivia, it has been recorded only four times in a total of about 300 vegetation plots (of which approximately 90 covered suitable early- to mid-successional vegetation) located in the right elevational belt within the distributional area of *Loxsomopsis* (M. Kessler, unpubl. data). In southeastern Ecuador, *Loxsomopsis* is locally common on roadsides (B. Øllgaard, pers. comm.).

#### TAXONOMIC TREATMENT

*Loxsomopsis* H. Christ, Bull. Herb. Boiss. II, 4:399. 1904.—Type: *Loxsomopsis costaricensis* H. Christ.

A monotypic genus, with the characteristics of its single species.

*Loxsomopsis pearcei* (Baker) Maxon, Proc. Biol. Soc. Wash. 46:105. 1933. *Dicksonia pearcei* Baker, Ann. Bot. (Oxford) 5: 197. 1891. *Dennstaedtia pearcei* (Baker) H. Christ, Index fil. 218. 1905.—Type: Ecuador, "Eastern Andes, 8000–9000ft." *Pearce 251* (Holotype, K!; Photo, US).

*Loxsomopsis costaricensis* H. Christ, Bull. Herb. Boiss. II, 4:399. 1904.—Type: Costa Rica, *Wercklé 279* (Holotype, P!).

*Loxsomopsis lehmannii* Hieron., Bot. Jahrb. Syst. 34:435. 1904.—Type: Ecuador, [Morona-Santiago,] prope Chinguinda, declivibus montium Cordillera Oriental de Sigsig, 1800–2500m, *Lehmann 5061* (Isotype, K!, US!). According to Tryon and Stolze (1989) holotype destroyed in LZ.

*Loxsomopsis notabilis* Slosson, Bull. Torr. Bot. Cl. 39:285. 1912.—Type: Bolivia, [La Paz, Franz Tamayo,] near Apolo, 6000 ft., *Williams 1303* (Holotype, US!; Isotypes, P!, US!).

Terrestrial fern with long-creeping, slender to rather stout, branched, solenostelic stem bearing stiff, dark brown, multicellular, basally pluriseriate bristles. Leaves remote, non-articulate, 0.3–1.5 m long. Petiole as long as to somewhat longer than lamina, with a single, gutter-shaped vascular bundle, adaxially convex to flattened-sulcate, with bristles at the base and sometimes further along the petiole. Lamina narrowly to broadly deltate, 1-pinnate-pinnatifid to bipinnate-pinnatifid, firm, catadromous, hypostomatic; pinnae (sub)sessile, subopposite, asymmetric, the basiscopic segments reduced, secondary pinnae and segments obliquely ascending, decurrent, ultimate segments deltoid-lanceolate, margin crenate to entire. Stomata paracryptic. Veins free, forked-subpinnate, catadromously branched. Sori terminal on a vein, protruding beyond the margin, directed downwards from plane of lamina, profusely paraphysate; sorus cyathiform to urceolate, laterally free; receptacle columnar. Sporangia on short, pluriseriate stalks; annulus almost vertical, continuous and 3/4 indurated. Spores trilete, 41–62  $\mu\text{m}$  in diameter, slightly pitted to verrucate, mostly granulate.

#### SPECIMENS EXAMINED

**COSTA RICA.** **Alajuela:** Shore of lake on Poás Volcano, 2500 m, *Lent 512* (F); Near edge of lake, Poás Volcano, 2500 m, *Lent 738* (F); Along shore of old crater lake of Volcán Poás, 2500 m, *Mickel 3654* (NY); Poás lake, 8500 ft., in sandy soil by lake shore, *Stork 2522* (US); Edge of small lake inside of an extinct sub-crater of Volcán Poás, about 11 km NW of Heredia, 2700 m, *Taylor 4496* (NY); Shore of lake, crater summit, Volcán Poás, 2600 m, *Weston 4624* (UC). **Heredia:** Volcán Barba, 6700 ft., *Evans 2660A* (MO, U, Z); Headwaters of Río Santo Domingo, ca. 3 km NE of San Rafael de Vara Blanca, N slope of Volcán Barba, 10° 11.5' N, 84° 07' W, 2060 m, *Grayum 7212* (MO, US); Bordes del Río Grande, afluyente del Río Patria, en el Paso del Gallito, macizo del Volcán Barba, 2045 m, *Jimenez 2272* (F, NY, UC, US); Southeast shoulder, near end of Route 113, 6 miles NNE of San Rafael de Heredia, *Lloyd s.n.* (MO, UC); San Jose, 10 km N of San Rafael de Heredia on Volcán Barba, 1950 m, *Mickel 3001* (UC, US); Río de las Vueltas, 2100 m, *Goldgewicht 863* (US); En el Río de las Vueltas, 2000 m, *Goldgewicht 86369* (CR); End of rt. 113, where road crosses Río Patria about 100–200 m upstream, 2000 m, *Moran 3051* (AAU). **Limón:** N flank of Cerro Casma, along Ujarrás—San José Cabécar trail, Cordillera de Talamanca, 09° 20' 30'' N, 83° 13' 30'' W, 2250–2270 m, *Grayum 10329* (CR, F, MO); P.I. La Amistad Valle de Silencio, 09° 07' 15'' N, 82° 57' 55'' W, 2450 m, *Moraga 339* (CR, UC). **Prov. unknown:** *Wercklé 225* (P).

**Colombia.** **Nariño:** Municipio de San Francisco, carretera Pasto-Mocoa, entre El Mirador y San Francisco, 1500–2200 m. *Mora 4449* (COL). **Norte de Santander:** Municipio de Toledo, de Toledo

a Samore, 2200 m. *Lozano et al.* 5472 (COL). **Putumayo:** road from San Francisco to Mocoa, km. 112 from Pasto, near El Mirador, 7200 ft. *Plowman* 4352 (COL).

ECUADOR. **Morona-Santiago:** Limón-Gualacco Road, km 16, 2100–2200 m, montane forest, *Harling* 24597 (QCA); Pica Sevilla de Oro-Mendez colecciones “entre Páramo del Castillo-Cerro Negro-Dominguillos”, 78° 34' W, 2° 47' S, 3000–3250 m, *Jaramillo* 5558 (AAU, QCA); Carretero Limón-Gualaceo, 35 km desde Olan de Milagro, Colecciones a lo largo de la carretera, 1800 m, *Navarrete* 600 (AAU, QCA); Muletrack Sevilla de Oro-Mendez, eastern slope (E of Cerro Negro, El Castillo), montane forest along muletrack, 78° 34' W, 2° 47' S, 2800–2950 m, *Ollgaard* 9479 (AAU, F); Sigsig, Chinguinda, 1500–2000 m, *Lehmann* 5059 (K, US); Sapote, 2100 m, *Crespi* 72 (US). **Azuay:** “Oriente” Border: Eastern Cordillera, between Oña and the Río Yacuambi, east slope, 8000–9000 ft., *Prieto* 259 (F, GH, K, MO, NY, US). **Zamora-Chinchipe:** Road Loja-Zamora, km 14, 79° 09' W, 4° S, 2750–2770 m, *Holm-Nielsen* 3860 (AAU, F, MO, NY); Eastern slopes of the East Andes of Loja, 2000–2500 m, *Lehmann* 5715 (K, US); Parque Nacional Podocarpus, around pass on road Loja-Zamora, 79° 07' W, 3° 58' S, 2750–2950 m, *Ollgaard* 74387 (AAU, K, NY, QCA); Road Loja-Zamora, just E of the pass, low scrub along old trail, 79° 10' W, 03° 58' S, 2800 m, *Ollgaard* 98820 (QCA); Strasse von Loja nach Zamora, Páramo del Nebula, Pass an der Grenze von Loja und Zamora-Chinchipe, 3600 m, *Schneider* 579 (Z); 10 km outside Loja along new road Loja-Zamora, just past the Nudo, 2900 m, *van der Werff* 9107 (AAU, MO, NY, UC); pass on road Loja-Zamora, ca. 15 km E of Loja, ca. 3005 m, *van der Werff* 13456 (MO); Parque Nacional Podocarpus, Road Yangana-Valladolid, km 26, 79° 09' W, 04° 29' S, 2550 m, *Madsen* 75754 (AAU, QCA); Parque Nacional Podocarpus, Road Yangana-Valladolid, just S and E of the pass (Nudo de Sabanilla), muletrack from pass toward Quebrada Honda, 78° 08' W, 4° 27' S, 2750–2950 m, *Ollgaard* 91061 (GOET), *Ollgaard* 90634B (AAU, QCA). **Santiago-Zamora:** Trail between Pailas and El Pan, 2255–3445 m, *Steyermark* 54324 (F, NY, US). (**Carchi:** Espejo, El Goaltal, Cerro Golondrinas, vegetacion arbustiva (matorral) espeso sobre la cresta de la montaña, bosque muy humedo montano bajo, 0° 51' N, 78 08' W, 2600–2800 m, *Palacios and Clark* 12463 (MO); not seen by us, but studied by A.R. Smith, pers. com.).

PERU. **Huanuco:** Southwestern slope of the Río Llulla Pichis watershed, on the ascent of Cerras del Sira, 9° 25' S, 74° 42' W, 2205 m, *Dudley* 13420 (GH); Playapampa, ca. 9000 ft., *Macbride* 4521 (F, GH, US). **Pasco:** Border Prov. Oxapampa and Pasco, 2700 m, *van der Werff* 8564 (MO, NY). **Cuzco:** Cachayocpata, entrada del Valle San Miguel La Convención, 10000 ft., *Bües* 2119 (US); La Convención 73° 34' W, 12° 37' S, 2555 m, *Dudley* 10713 (GH, MO).

BOLIVIA. **La Paz:** Nor Yungas, 5 km de Chuspipata hacia Coroico, 16° 23' S, 67° 48' W, 2750 m, *Kessler* 11981 (UC, GOET); Nor Yungas, Chuspipata, camino sobre loma de montaña a Coroico, 16° 18' S, 67° 49' W, 3000 m, *Lehnert* 032 (LPB, UC, GOET); Nor Yungas, entre Cotapata y Chuspipata, 16° 18' S, 67° 50' W, 3100 m, *Smith* 13139 (F, MO, UC). **Cochabamba:** José Carrasco Torrico, 112 km antigua carretera Cochabamba-Villa Tunari, 17° 07' S, 65° 38' W, 2700 m, *Kessler* 6928 (UC); José Carrasco Torrico, 130 km antigua carretera Cochabamba-Villa Tunari, 17° 07' S, 65° 36' W, 2000 m, *Kessler* 7209 (UC, GOET).

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